ECOPHYSIOLOGICAL STRATEGIES OF TERRESTRIAL ARTHROPODS FOR SURVIVING HEAVY METAL POLLUTION

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INTRODUCTION

One of the most severe problems which faced the early invertebrate colonisers of land was the regulation of uptake and excretion of essential and non-essential metals. These animals were no longer bathed in seawater with its plentiful supply of essential metal ions and limitless sink for unwanted substances. The midgut epithelium became the only site of exchange of metals between the blood and the food. Consequently, a thorough knowledge of how the digestive system functions is of paramount importance if we are to understand how metal concentrations are regulated within terrestrial arthropods. There are three main factors which control the extent to which the different groups of terrestrial arthropods accumulate metals. First, the diet, second, the structure and physiology of the digestive system and third, the mechanisms by which metals are stored within cells in an insoluble form.

1. Diet

The concentrations and chemical forms of metals in the food are the first factors which influence the extent of metal accumulation by terrestrial arthropods. Metals contaminating plant material in an aerially polluted site will be present mostly as fine particles on leaf surfaces. Metals in this form are more 'available' to herbivores than the same concentrations in the same plant species at a site where soil is enriched with metals as a result of mining activity. In such sites, the metals have entered the plants via the roots and are bound firmly to organic ligands within the leaf tissues.

The extent to which carnivorous invertebrates ingest metals depends not only on the choice of prey species but also on the parts of the prey which are eaten. For example, spiders of the genus _Dysdera_ exist exclusively on a diet of terrestrial isopods. In contaminated sites, the hepatopancreas (midgut gland) of isopods may contain the highest concentrations of zinc, cadmium, lead and copper recorded in any terrestrial invertebrate (Hopkin and Martin, 1984). When the spider catches an isopod, it injects its prey with enzymes and sucks out the digested soft tissues. Since these tissues include the hepatopancreas which contains most of the metals in the isopod, the concentrations of metals in the diet of the spider are much greater than an analysis of

concentrations in whole woodlice would suggest (Hopkin and Martin, 1985). In contrast to its isopod prey, Dysdera can not adopt the strategy of permanent storage to detoxify metals because the capacity of the midgut gland cells would soon be exceeded. Therefore after each meal, Type A and Type B metal-containing intracellular granules which have formed in the midgut (see Fig. 1), are excreted by lysis of the cells. Large numbers of these granules are present in the faeces (Hopkin, personal observation).

Lithobiid centipedes have a more simple digestive system with no midgut diverticulae. When these animals are fed on the hepatopancreas of isopods, they are unable to digest the metal-containing granules of the woodlice which are voided in the faeces, apparently unchanged (Hopkin, personal observation).

2. Structure and Physiology of the Digestive System

Topologically, the midgut of all terrestrial arthropods can be considered to be an open-ended cylinder joined to the cuticle-bearing ectoderm near the mouth and the anus. There are however several invertebrate groups which have increased the surface area of the midgut in contact with the food, and the potential storage capacity for metals, by the development of diverticulae. The chemical conditions within the lumen of different regions of the gut may differ radically along its length. In larvae of the dipteran Lucilia cuprina, copper and iron are only absorbed in a small region of the midgut where the pH of the gut contents is less than 4, significantly below the neutral pH of the rest of the midgut lumen (Waterhouse and Stay, 1955). Other factors that will effect metal uptake include the presence of a peritrophic membrane and/or a population of microorganisms which can either promote or repress metal assimilation (Simkiss, 1985).

3. Intracellular Storage Mechanisms

Many papers have been published on metal-containing inclusions in invertebrates (for a review of this topic see Taylor and Simkiss, 1984). It is clear from studies on marine invertebrates that the basic systems for transport and storage of metals were evolved long before the land was colonised. In Fig. 1, I have proposed a classification system for these inclusions which is based on the Lewis acid properties of the metals they contain rather than their structure in two dimensional sections which has led to confusion in the past (for a discussion of the 'hard', 'soft' and 'borderline' metal ion concept, see Nieboer and Richardson, 1980). These 'granules' fall into four categories.

Type A granules are composed of concentric rings of calcium phosphate (probably pyrophosphate) and rarely exceed 3 µm in diameter. Class A ('oxygen-seeking') metals such as

manganese, and borderline metals such as zinc may be present.

Type B granules reach a similar size to type A granules and are composed of class B ('sulphur-seeking') metals such as copper, cadmium, mercury, and silver, and borderline metals such as zinc together with large amounts of sulphur. These granules may be modified lysosomes possibly formed from residues of metal-binding proteins such as the cysteine-rich metallothioneins.

Type C granules are composed almost entirely of iron and may represent breakdown products of the iron-storage protein ferritin. In sites contaminated with heavy metals, they may also contain zinc and lead (Hopkin and Martin, 1984).

Type D granules are most frequently seen in molluscs but have yet to be discovered in terrestrial arthropods. They are included in this scheme because when small, they have a similar appearance to Type A granules. However, unlike Type A granules, Type D granules are extracellular, may reach a diameter of greater than 20 μm and are composed of calcium carbonate. In molluscs, they probably exist to buffer the pH of the blood (Taylor and Simkiss, 1984).

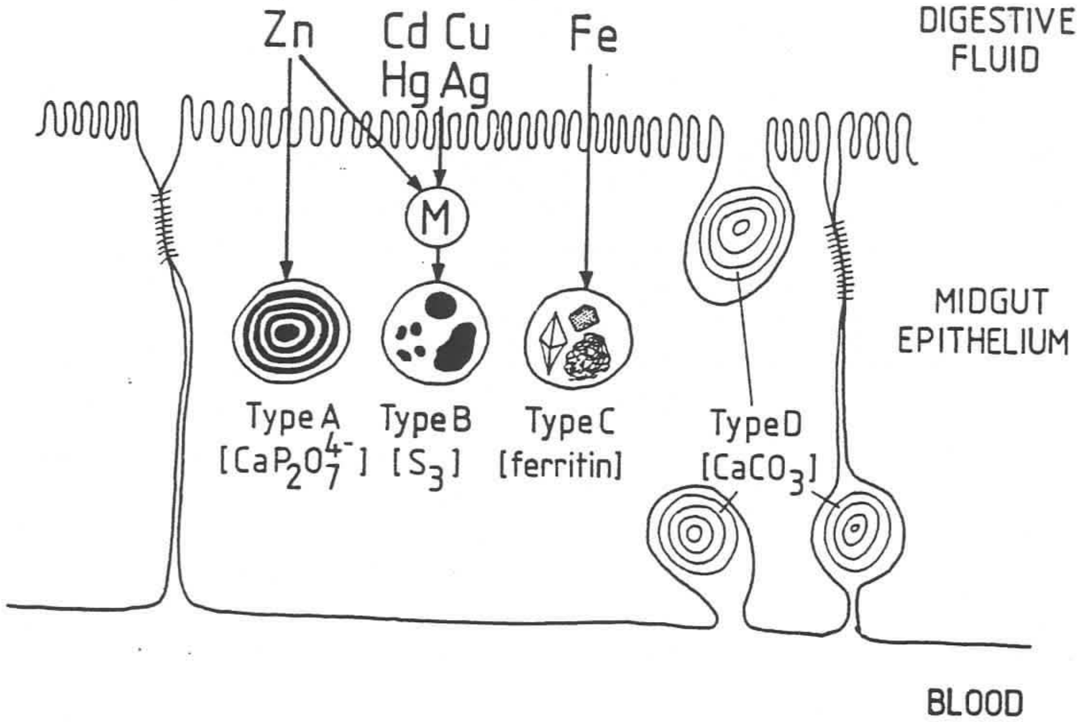

Fig. 1. Schematic diagram of the four types of metal-containing granules found in the midgut of invertebrates. Types A, B and C are intracellular and are contained within a membrane. Type D granules are extracellular. Metals may be transported to granules by metallothionein proteins (M).

CONCLUSIONS

There is no evidence to demonstrate categorically that once Type A, B and C granules are formed they can be re-dissolved. Thus they probably represent a true storage-detoxification system. The 'choice' as to whether to retain the granules within the midgut cells (a strategy employed by terrestrial isopods) which probably involves the expenditure of less energy than would be required to pump metals out, or whether to excrete them by lysis of midgut cells and their contents (a strategy employed by Dysdera) is probably dictated by the factors outlined in this review. First, what are the concentrations and forms of metals which are present in the midgut lumen of the animal? These depend on the type and specific parts of food which are eaten and on the activity of digestive enzymes. Second, does the structure and physical capacity of the midgut cells provide sufficient 'room' for permanent storage of metals which enter the cells during the normal lifespan of the animal?. Third, does the animal possess mechanisms for intracellular storage which enable it to bind unwanted metals in a non-toxic form? In heavily polluted sites, the ability to regulate metals by such mechanisms is probably the main selective pressure acting on terrestrial invertebrates (Hopkin et al, 1986).

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